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FLUCTUATIONS IN THE POPULATIONS, WEIGHTS AND BIOMASSES OF ANTS AT THORNHILL, YORKSHIRE, FROM 1935 TO 1939

By Walter Pickles.

Communicated by Dr. O. W. Richards, F.R.E.S.

With Five Text-figures.

Manuscript received 14th January, 1940.

(Read 5th June, 1940.)

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1. Introduction.

A survey of the colonies of three species of ants was carried out on a hillside at Thornhill near Dewsbury (Yorkshire), during the summer months of the years 1935 to 1939. The fluctuations in the populations and the weights and biomasses of the ants were recorded during this period.

The area of ground was particularly suitable for ant activity, as it consisted chiefly of a steep slope rising about 1 in 2 and facing south-south-east. The surface consisted chiefly of the exposed sub-soil of sandstone with its loose, somewhat irregularly rectangularly shaped flat flags of small size. There was practically no depth of soil, the stones and soil forming the surface of the ground at that point.

The vegetation consisted mainly of a thick growth of bracken (*Pteris aquilina*) with odd patches of brown knapweed (*Centaurea Jacea*), gorse (*Ulex europaeus*), the grasses *Holcus mollis*, *Aira flexuosa* and *Agrostis alba*. Intertwining amongst the bracken were the stems of the bramble (*Rubus fruticosus*).

The species of ants studied there were *Lasius flavus* Fab., *Formica fusca* L. and *Myrmica ruginodis* Nyl.

2. Discussion of the Ants' Nests.

Throughout the five summers during which the survey was made, a total of 78 ants' nests has been recorded on an area of ground 1052 square yards in extent. Some of the nests have been inhabited for only one year and never

again, whilst some of them have been re-inhabited over two or more years by the same species of ant or by a different one. Details of these are given in Table 1.

TABLE 1.

Nest no.	1	1935–37, *L. flavus*; 1938, *L. flavus–M. ruginodis–F. fusca*; 1939, *F. fusca*.
,,	2	1935–37, *F. fusca*.
,,	3	1935–39, *L. flavus*.
,,	5	1935–36, *M. ruginodis*.
,,	6	1935–37, *F. fusca*.
,,	8A	1936–37, *M. ruginodis*.
,,	13	1935–36, *F. fusca*.
,,	14	1935–37–39, *M. ruginodis*.
,,	20	1936–37, *M. ruginodis*.
,,	21	1936–37, *M. ruginodis*; 1938–39, *L. flavus*.
,,	26	1937–38, *L. flavus*.
,,	34	1938–39, *F. fusca*.
,,	46	1938–39, *F. fusca*.
,,	50	1938–39, *L. flavus*.

From this table it is evident that of all the 78 ants' nests which have existed on the area of ground under survey, 14 have been inhabited for more than one year. This table also shows that although a nest has been inhabited for more than one year, it has not always been inhabited by the same species. *L. flavus* has been most tenacious of one spot. Nest no. 1 was inhabited by this species of ant from 1935 to 1938, and no. 3 during all the five years. As this species of ant builds its nest-mound by adding grains of soil to the top, as described by Donisthorpe (1927), and owing to the fact that the secretion of the mandibular glands, which according to Imms (1934) function as salivary glands and may coat the particles of soil used in building and so make them alkaline (Janet, 1898), it would tend to make this soil chemically recognisable from the surrounding soil.

Janet (1898) states that the soil of ants' nests, and mentions *Lasius* in particular, is made more alkaline by the ants. This has been confirmed by Pickles (1940) by comparing the pH of the soil of the ants' nests with that of the soil surrounding them.

Wigglesworth (1927) gave the pH of the saliva of the wild cockroach as 6·9. I found (1940) that there was an average difference of 0·6 pH unit throughout the summer of 1939 between the pH of the soil of the hillside and that of the nest-mounds of *L. flavus* (hillside soil average pH = 4·4; nest soil = 5·0). A pH of 6·9 or so for the saliva of ants would help to account for the decided and varying degree of greater alkalinity of the soil of the ants' nests than that of the surrounding soil of the hillside.

I am inclined to suggest that *L. flavus* in particular will be able to recognise an old nest-mound in this way, and so tend to re-inhabit it over two or more years (five years in the case of nest no. 3).

Out of the 78 nests which have been investigated, some were found to be permanent ones, in the sense that they were inhabited during the whole of one particular season. The rest were only inhabited for short periods and then deserted. These have been called temporary nests. This indicates that the ant population of the area must be on the move from one stone or mound to another. As mentioned above, *L. flavus* is the most stationary, or at least returns to previously inhabited nests most often. On other parts of the hillside, mounds of this species of ant have existed for a number of years. There is no doubt that the mound of nest no. 1 would still have been in a flourishing

condition in 1939 if it had not been subjected to repeated digging to enable a census to be taken.

There is another point that makes itself evident from the plan of the nests, fig. 1, and that is, that they have been most crowded together in one part, and not equally distributed over the area as might be expected. The reason for this is, probably, because around nests 41, 55, 69, 74, etc. there is a greater preponderance of loose flat stones than anywhere else on the area. It will be noticed that the nests are practically all either *M. ruginodis* or *F. fusca*; there being five of *L. flavus* (*i.e.* nos. 3, 54, 55, 42 and 65) to twenty-one of the other two species.

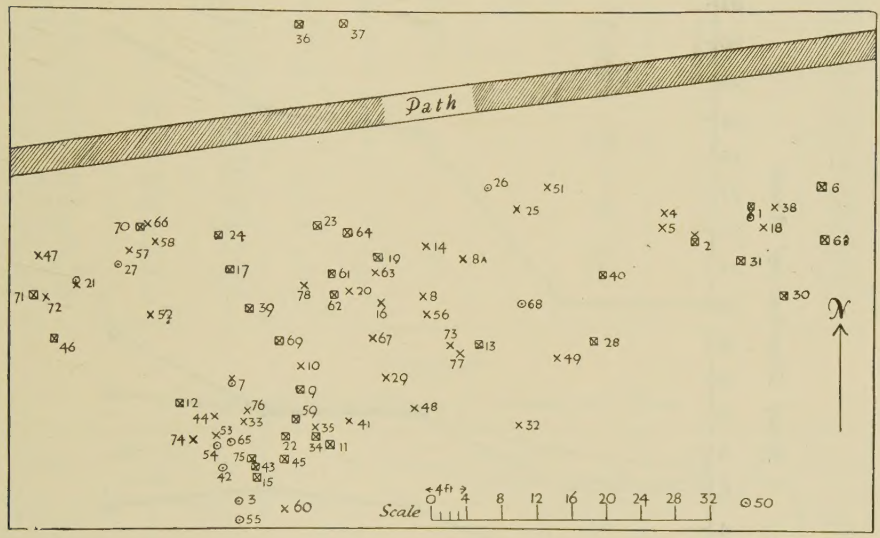

FIG. 1.—Plan of the nests on the area under survey. ⊙ nests of *L. flavus*; ⊠ nests of *F. fusca*; × nests of *M. ruginodis*; ⊙× mixed nests of *L. flavus–M. ruginodis*; ×⊠ mixed nests of *F. fusca–M. ruginodis*, and ⊠⊙ mixed nests of *L. flavus–F. fusca–M. ruginodis*.

In fig. 2 graphs of the total number of nests are shown. From this it will be seen that the total number of nests has increased during the time of the survey. In 1935 there was a total of 16 nests, whilst in 1939 the number had about doubled, *i.e.* 30. *M. ruginodis* and *F. fusca* have also increased in numbers, and the great increase in the total number of nests in 1939 was due to the greater number of nests of these two species (11 of *F. fusca* and 14 of *M. ruginodis*) as against 10 of each of these species in 1938. *L. flavus* had its peak year in 1938 with 6 nests; the total for this species fell to 5 again in 1939.

3. Types of Nests.

L. flavus: The mounds of *L. flavus* have been built up above the sub-soil, which is composed of small flat stones, by the addition of soil carried up on to the mound as described by Donisthorpe (1927). The bases of these nests are among the stones of the sub-soil; but the mound stands up above the general level of the soil. This superstructure is drier than the rest of the

ordinary soil of the hillside. Most of the mounds are covered with the grass *Aira flexuosa* with sprinklings of *Holcus mollis*.

M. ruginodis : The nests of this species of ant were always made under flat stones and then a layer of soil was prepared beneath it which was usually mixed with foreign matter. This foreign matter, which was used for building, consisted partly of the seeds of the grass *Aira flexuosa*. The soil of one nest produced a considerable number of small green pellets. These were found to be composed of masticated blades of grass, and on microscopical examination the grass *Holcus mollis* was identified among the fragments from the pellets.

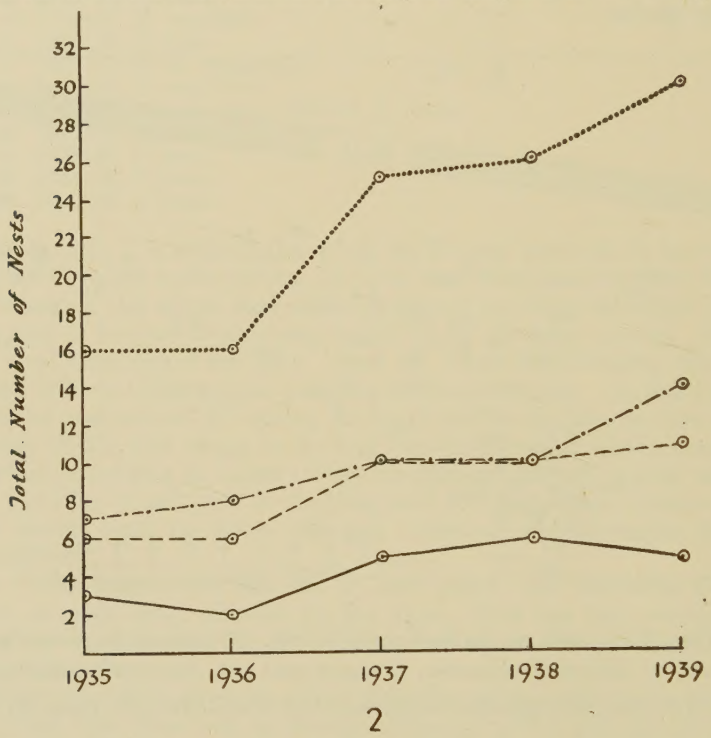

Fig. 2.—The fluctuation of the total number of nests on the area during the five summers of the survey. — — — *F. fusca*; ——— *L. flavus*; .—.—.— *M. ruginodis*; ..... Total number of nests of all species for each year.

F. fusca : The nests of this species of ant were all made under flat stones. Beneath the edges of the stones, a boundary " wall " was built of various materials, chiefly the seeds of the grass *Aira flexuosa* and also small dead fragments of bracken fronds. One nest was found to be completely made up of the broken fragments of bracken fronds below the stone. Small pellets of earth were also found amongst the vegetable matter, as part of the building material. In some cases the boundary " wall " of the nests contained many empty pupae cases. Andrews (1929) mentions that he found *Formica exsectoides* Fab. using pupae cases as building materials.

4. Populations.

In Tables 2, 3 and 4 analyses of the populations of the ants' nests on the area are given for the whole five seasons. The undisturbed nests of *L. flavus*

had the largest populations. The two mounds were big and, as was to be expected, the populations were large, though the size is by no means a guide to

TABLE 2.

Analysis of the populations of the nests of *L. flavus*.

Date	No. of nest	☿	♂	♀	Larvae	Naked pupae	☿ cocoons	♀ cocoons	Callows	Total
9.viii.35	3	3880	641	33	90	—	877	—	92	5613
5.x.35	1	5240	141	362	—	—	—	—	—	5743
19.ix.36	1	1388	4	72	74	—	5	—	—	1543
11.vii.36	3	1722	—	1	152	—	274	61	—	2210
10.vii.37	3	1333	2	1	16	—	124	5	—	1481
11.viii.37	21	1763	25	3	—	—	78	—	—	1869
25.viii.37	1	152	—	—	—	—	—	—	—	152
8.ix.37	27	1127	—	1	—	—	—	—	—	1128
23.vii.38	21	1548	—	1	—	—	470	3	—	2022
19.viii.38	1	135	—	—	—	—	—	—	—	135
10.ix.38	42	665	140	1	—	—	5	—	—	811
17.ix.38	55	504	19	—	—	—	83	—	—	606
15.x.38	50	1687	51	1	—	—	—	—	—	1739
24.vi.39	65	467	—	—	42	—	163	—	—	672
4.viii.39	50	1693	72	13	—	—	343	—	16	2137
30.ix.39	21	371	137	9	—	—	—	—	—	417

TABLE 3.

Analysis of the populations of the nests of *F. fusca*.

Date	No. of nest	☿	♂	♀	Larvae	Naked pupae	☿ cocoons	♀ cocoons	Callows	Total
29.viii.35	6	172	—	1	—	—	84	—	18	275
30.viii.35	12	50	—	1	—	—	18	—	4	73
30.viii.35	9	190	—	1	—	—	22	—	5	218
7.ix.35	11	65	—	—	—	—	—	—	—	65
21.ix.35	13	115	—	1	—	—	27	—	—	143
21.ix.35	2	248	—	1	—	—	30	—	—	279
18.vii.36	6A	204	—	1	3	—	124	6	—	338
6.viii.36	6B	131	—	—	—	—	249	2	—	382
7.viii.36	17	635	—	28	—	—	85	—	18	766
18.viii.36	13	170	—	1	63	—	113	—	5	352
26.viii.36	2	173	—	1	32	158	105	—	13	482
3.x.36	19	13	—	—	—	—	—	—	—	13
17.x.36	15	56	—	—	—	—	—	—	—	56
4.viii.37	30	326	—	1	43	127	112	—	—	609
27.viii.37	31	333	—	1	—	—	8	—	—	342
25.ix.37	36	603	—	4	—	—	31	—	—	638
20.x.37	37	189	—	—	—	—	—	—	—	189
19.viii.38	34	333	—	—	—	103	111	—	—	547
19.viii.38	1	36	—	—	—	—	—	—	—	36
3.ix.38	43	129	—	1	—	47	33	—	—	210
10.ix.38	44	18	—	1	—	—	6	—	—	25
17.ix.38	46	272	—	—	—	—	—	—	—	272
31.vii.39	70	134	—	1	21	32	5	—	—	193
25.viii.39	71	110	—	1	—	2	30	—	—	143
9.ix.39	46	48	—	1	—	—	12	—	—	61
16.ix.39	34	216	—	1	—	—	22	—	2	241
23.ix.39	64	33	—	1	—	—	7	—	—	41

TABLE 4.

Analysis of the populations of the nests of *M. ruginodis*.

Date	No. of nest	☿	♂	♀	Larvae	Naked pupae	☿ cocoons	♀ cocoons	Callows	Total
31.viii.35	10	1281	4	—	249	—	—	—	—	1534
21.ix.35	2	248	—	1	—	30	—	—	—	279
7.ix.35	14	171	—	1	52	9	—	—	—	233
30.ix.35	8	623	—	1	36	—	—	—	—	660
26.viii.36	2	78	—	—	—	—	—	—	—	78
20.viii.36	5	854	—	23	84	148	—	—	50	1159
30.viii.36	18	451	—	38	—	—	—	—	—	489
3.x.36	8A	278	—	—	65	—	—	—	—	343
17.x.36	21	35	—	—	—	—	—	—	—	35
19.viii.37	29	93	—	—	14	5	—	—	—	112
6.viii.37	8A	185	—	2	—	—	—	—	—	187
11.viii.37	21	28	24	—	—	—	—	—	—	52
11.ix.37	32	456	—	1	—	—	—	—	—	457
18.ix.37	33	878	—	1	20	—	—	—	—	899
25.ix.37	35	457	—	—	—	—	—	—	—	457
3.viii.38	41	554	—	1	—	70	—	—	—	625
19.viii.38	1	1192	2	1	—	—	—	—	—	1195
24.viii.38	48	482	—	1	42	24	—	—	—	549
26.viii.38	49	487	12	3	—	—	—	—	—	502
3.ix.38	52	101	—	—	—	—	—	—	—	101
10.ix.38	53	655	—	1	58	—	—	—	—	714
17.ix.38	51	704	2	—	—	—	—	—	—	706
1.x.38	47	1124	8	4	93	—	—	—	—	1229
29.iv.39	57	984	—	5	—	—	—	—	—	989
23.viii.39	74	568	7	1	—	38	—	—	—	614
9.ix.39	78	281	—	2	—	—	—	—	—	283
16.ix.39	72	77	—	2	—	—	—	—	—	79
23.ix.39	56	799	—	2	—	—	—	—	—	801
7.x.39	66	274	—	—	—	—	—	—	—	274

the size of the populations. Andrews (1929) mentions that he found the same thing, namely, that the size of the mound does not always give an indication of the size of the population. This is particularly true about the other two species, a large stone may cover a small nest and vice versa (see Pickles, 1936 and 1937).

In the large mounds of *L. flavus* the populations were more or less distributed with a definitely greater congregation towards the upper and outer parts of the mounds. In the nests of *M. ruginodis*, the distribution of the ants in the nests seems to have been vertically downwards from the stone to a depth, in some cases, of eighteen inches, or more. *F. fusca* had a more horizontal distribution, as a rule using up most of the underside of the stone covering the nest.

The populations of the nests have fluctuated greatly during the five years' survey. *L. flavus* had its maximum population in 1935. The disturbing of the two original nests seems to have had an adverse effect on their populations. The smallest population was in 1939. From 1936 there was an increase in population until 1938, from which date there was a decrease.

F. fusca had its peak of population in 1936. Since then the populations have shown a steady decline. It seems probable that, at the present rate of decrease, the species would be shortly non-existent on the area, that is, of course, leaving out the fact that there may be immigrations from the surrounding regions, which is more than a probability.

M. ruginodis had its maximum population in 1938 and its minimum in 1936. In 1939 this species showed a tendency to decrease in numbers again.

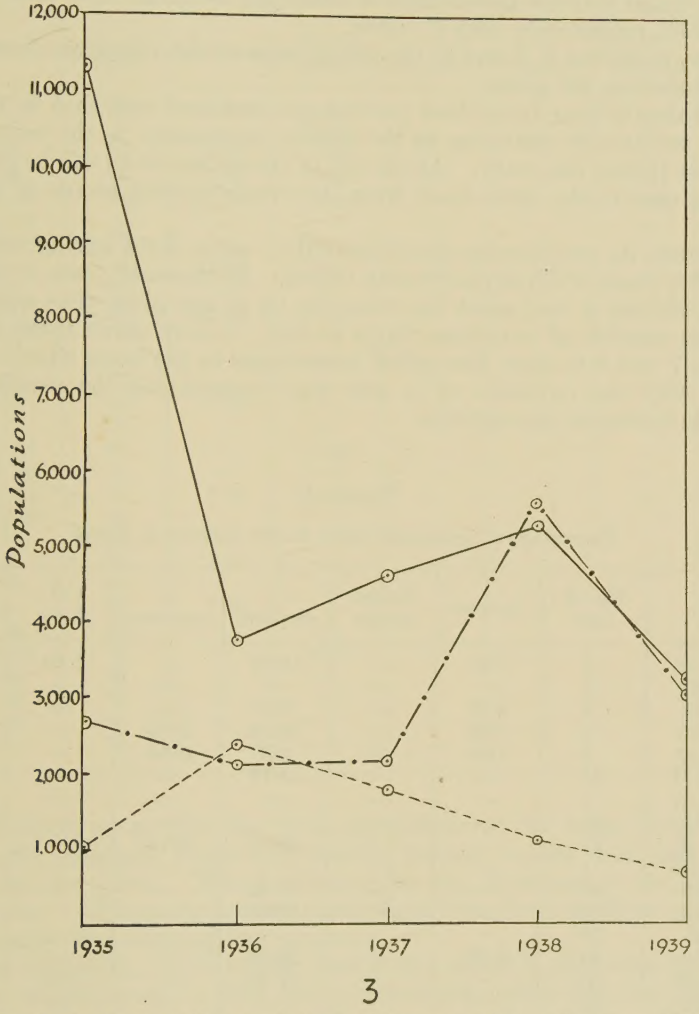

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FIG. 3.—The fluctuations of the populations of the nests during the years 1935 to 1939. ——— *L. flavus*; — — — *F. fusca*; ·—·—·— *M. ruginodis*.

In Table 5 and fig. 3, the fluctuations of the total populations for the five summers are shown.

TABLE 5.

The fluctuations of the total populations of all three species.

Species	1935	1936	1937	1938	1939
L. flavus	11356	3753	4630	5313	3226
M. ruginodis	2706	2104	2164	5621	3040
F. fusca	1053	2389	1778	1090	679

It is mentioned by Andrews (1929), that Eidman found in *L. niger* that the proportion of immature to mature ants in the nests was 75%. Young and Andrews found that the percentages of immature to mature ants were 25% and 33% to 50% respectively with *F. rubra*.

Below, in Tables 6, 7 and 8, the percentages of the immature forms to the total populations are given.

One thing is clear from these percentages in a nest and that is, that they must be continually changing as the season progresses; as the proportion of the larvae, pupae, etc., vary. At the end of the season there will be practically no young ones in the nests apart from the over-wintering larvae of autumnal eggs.

The nests do not develop simultaneously: some nests having young ones in a further stage of development than others. As this is the case, it is difficult to know whether a nest which has been dug up at any given time contains the maximum number of immature forms or not. I have given these results in Tables 6, 7 and 8 to show the actual percentages in the nests which were dug up, not with the intention of in any way representing the percentages of maximum immature populations.

TABLE 6.

Percentage of immature forms in the nests of *L. flavus*.

Date	No. of nest	Larvae	Naked pupae	♀ cocoons	♀ cocoons	Callows	Total
9.viii.35	3	1·60	—	15·62	—	1·64	18·86
5.x.35	1	—	—	—	—	—	—
19.ix.36	1	4·80	—	0·32	—	—	5·12
11.vii.36	3	6·88	—	12.39	2·76	—	22·03
10.vii.37	3	1·08	—	8·37	0·34	—	9·79
11.viii.37	21	—	—	4·17	—	—	4·17
25.viii.37	1	—	—	—	—	—	—
8.ix.37	27	—	—	—	—	—	—
23.vii.38	21	—	—	23·24	0·15	—	23·39
19.viii.38	1	—	—	—	—	—	—
10.ix.38	42	—	—	0·62	—	—	0·62
17.ix.38	55	—	—	13·69	—	—	13·69
15.x.38	50	—	—	—	—	—	—
24.vi.39	65	6·25	—	24·26	—	—	30·51
4.viii.39	50	—	—	16·05	—	0·75	16·80
30.ix.39	21	—	—	—	—	—	—

In only three nests (*i.e.* nos. 2, 6B and 13), during the year 1936, all nests of *F. fusca*, do the figures of the immature and the adult forms give the pyramid shape of Bodenheimer's (1938) figure, indicating an increasing population. All the rest of the nest populations show the characteristic urn-shape which Bodenheimer (1938) described as illustrating dwindling populations. This means, then, from the fact that the populations have risen to a peak during the survey, that ants must have come into the area from the region outside.

The dwindling population of *F. fusca* may be due to two causes, (a) this general decrease associated with the fewer immature forms in the nests and (b) emigrations of this species not being balanced by immigrations from the surrounding area.

TABLE 7.

Percentages of immature forms to total populations of nests of *M. ruginodis*.

Date	No. of nest	Larvae	Naked pupae	♀ cocoons	♀ cocoons	♀ callows	Total
31.viii.35	10	16·23	—	—	—	—	16·23
21.ix.35	2	—	10·75	—	—	—	10·75
7.ix.35	14	22·32	3·86	—	—	—	26·18
30.ix.35	8	5·45	—	—	—	—	5·45
20.viii.36	5	7·25	12·77	—	—	4·31	24·33
26.viii.36	2	—	—	—	—	—	—
30.viii.36	18	—	—	—	—	—	—
3.x.36	8A	18·95	—	—	—	—	18·95
17.x.36	21	—	—	—	—	—	—
19.vii.37	29	12·50	4·46	—	—	—	16·96
6.viii.37	8A	—	—	—	—	—	—
11.viii.37	21	—	—	—	—	—	—
11.ix.37	32	—	—	—	—	—	—
18.ix.37	33	2·22	—	—	—	—	2·22
25.ix.37	35	—	—	—	—	—	—
3.viii.38	41	—	11·20	—	—	—	11·20
19.viii.38	1	—	—	—	—	—	—
24.viii.38	48	7·65	4·37	—	—	—	12·02
26.viii.38	49	—	—	—	—	—	—
3.ix.38	52	—	—	—	—	—	—
10.ix.38	53	8·12	—	—	—	—	8·12
17.ix.38	51	—	—	—	—	—	—
1.x.38	47	7·56	—	—	—	—	7·56
29.iv.39	57	—	—	—	—	—	—
23.viii.39	74	—	6·19	—	—	—	6·19
9.ix.39	78	—	—	—	—	—	—
16.ix.39	72	—	—	—	—	—	—
23.ix.39	56	—	—	—	—	—	—
7.x.39	66	—	—	—	—	—	—

In Table 9, on p. 476, the total populations of the nests of each species for the five summers which were carried forward to the next season during the winter, are given. This is allowing for the departure of the alate males and females. The over-wintering populations here given are those which would have resulted if no digging had occurred.

From this table, it will be seen that in the case of *L. flavus* the digging up of the two original nests in 1935 had a devastating effect on their populations which, instead of remaining at 10,000 or so, were about 3000. The winter of 1937–38 seems to have been one with little upset, as the wintering population and that found on the area in the following spring were about the same. The figures given for the wintering populations and the evidence for their over-wintering is based on Lubbock (1888). The effect of digging up the nests of *L. flavus* besides causing the great reduction of the populations of the original nests (by 1938 nest no. 1 was reduced to nil and later re-inhabited), has probably caused the ants to spread over the area, as in 1935 there were only two nests on the area whereas in 1938 there were six.

This seems to indicate that the repeated digging up of nests is not a suitable technique for the study of populations of a particular nest of this species.

With the other two species, the discrepancies between the actual wintering populations and those found in the nests at the beginning of the next year

could be attributed to the greater migration of these ants, considerable numbers probably having immigrated to the area. In the case of *F. fusca* a steady emigration appears to be taking place.

TABLE 8.

Percentage of immature forms in the nests of *F. fusca*.

Date	No. of nest	Larvae	Naked pupae	♂ cocoons	♀ cocoons	Callows	Total
29.viii.35	6	—	—	30·55	—	6·55	37·10
30.viii.35	12	—	—	24·66	—	5·48	30·14
30.viii.35	9	—	—	10·09	—	2·29	12·38
7.ix.35	11	—	—	—	—	—	—
21.ix.35	13	—	—	18·88	—	—	18·88
21.ix.35	2	—	—	10·75	—	—	10·75
18.vii.36	6A	0·89	—	36·69	1·78	—	39·36
6.viii.36	6B	—	—	65·18	0·52	—	65·70
7.viii.36	17	—	—	11·09	—	2·35	13·44
18.viii.36	13	17·89	—	32·10	—	1·42	51·41
26.viii.36	2	6·64	32·78	21·78	—	2·69	63·89
3.x.36	19	—	—	—	—	—	—
17.x.36	15	—	—	—	—	—	—
4.viii.37	30	7·06	20·85	18·37	—	—	46·28
27.viii.37	31	—	—	2·34	—	—	2·34
25.ix.37	36	—	—	4·86	—	—	4·86
2.x.37	37	—	—	—	—	—	—
19.viii.38	34	—	18·83	20·29	—	—	39·12
19.viii.38	1	—	—	—	—	—	—
3.ix.38	43	—	22·38	15·71	—	—	38·09
10.ix.38	44	—	—	24·00	—	—	24·00
17.ix.38	46	—	—	—	—	—	—
31.vii.39	70	10·88	16·58	2·59	—	—	30·05
25.viii.39	71	—	1·39	20·98	—	—	22·37
9.ix.39	46	—	—	19·67	—	—	19·67
16.ix.39	34	—	—	9·13	—	0·83	9·96
23.ix.39	64	—	—	17·07	—	—	17·07

TABLE 9.

The total over-wintering populations of the ants' nests. The figures in brackets give the actual populations at the beginning of the following season.

Species	1935–36	1936–37	1937–38	1938–39	1939–40
L. flavus	10,182	3617	4596	5103	2996
	(3112)	(4377)	(4542)	(2532)	
M. ruginodis	2702	2045	2140	5591	3029
	(1698)	(2101)	(5304)	(2990)	
F. fusca	1053	2354	1775	1090	679
	(1386)	(1454)	(790)	(546)	

5. TERRITORIES OF THE ANTS.

The ants leave their nests to go foraging for food. Two of the species studied (*M. ruginodis* and *F. fusca*) do so above ground chiefly (*M. ruginodis*

has been found attending the aphid *Tetraneura ulmifoliae* Bak. on the root of *Holcus mollis*). The extent to which they travel was found by following them from their nests and measuring the maximum distances travelled.

On the other hand, *L. flavus* seems to have only an underground territory. During the early part of the survey, owing to this underground territory being not taken into account, no territorial estimations were made (see Pickles, 1937 and 1938). That this was an error was pointed out by Carey and Diver (1937), and in 1937 a preliminary record of the underground territory of this ant was made (Pickles 1938). In 1938 a more definite figure was reached for the territory. As with the other two species, the territory was calculated from the maximum distance that the ants were found to have travelled away from the nest. To get this figure the ground was dug up, starting from the nest and spreading out in all directions from it. The positions of individuals or clusters of ants were measured up until no more were found. Nest 21 was used for this purpose as it was isolated from the others, and therefore when no more ants were discovered on digging further it was concluded that the boundary of the territory had been reached. The nearest neighbouring nests of this species were nos. 42 and 54; but they were far enough away for their territories not to overlap. The maximum distance travelled by these ants, underground, was 12 feet, and this gave a territory of 50·3 square yards. A continuation of the method described above failed to give a greater area of territory in 1939.

The maximum distances noted for the other two species were, for *F. fusca* 26 feet, giving an area of territory of 236 square yards; for *M. ruginodis*, 10·25 feet, which gave a territory of 36·7 square yards in extent.

6. Densities of Population.

Elton (1932) suggests that the density of population may be expressed in three ways: (a) the Economic Density (*i.e.* the total population of the area divided by the total foraging territory of the species); (b) the Lowest Density (*i.e.* the total population divided by the area of the census, 1052 square yards) and (c) the Greatest Density. This latter is taken as the population of the nests at night. As the nests were dug up either in the early morning or evening, the total populations given may be counted as their Greatest Densities.

In past reports on this survey (Pickles 1936, 1937, 1938), the population used for estimating the population densities have been taken as the total populations of the nests minus the pupae (these not being fed). No account was made of the variations of the populations in the nests at different times of the season. At the beginning of the season there were only adults in the nests in most cases; later there was the sequence of immature forms at varying stages of development. At the end of the season there were only adults again in the majority of cases, with the exception of over-wintering eggs, which were not found in the nests examined. Also the sexual winged forms had left the nests.

I have given results, in Table 10, of the variation in the Economic and Lowest Densities at the beginning of the season, in the period August to October (when there is the greatest number of immature forms in the nests) and again for the over-wintering period, in accordance with the details given above.

From this table, it may be seen that the highest recorded Economic Density was in 1935 for *L. flavus*, in 1937 for *F. fusca* and in 1935 and 1938 for *M. ruginodis*. Similarly, the highest recorded Lowest Densities were in 1935 for *L. flavus*, in 1936 and 1937 for *F. fusca* and in 1938 for *M. ruginodis*.

TABLE 10.

The densities of the populations. Ants per square yard.

	Spring		August–October		Winter	
	Economic density	Lowest density	Economic density	Lowest density	Economic density	Lowest density
1935						
L. flavus .	90·675	8·671	104·165	9·961	101·203	9·678
F. fusca. .	0·597	0·803	0·615	0·828	0·744	1·001
M. ruginodis .	15·845	2·211	18·167	2·535	18·406	2·568
1936						
L. flavus .	30·930	2·958	33·925	3·244	36·566	3·496
F. fusca. .	0·979	1·317	1·092	1·471	1·662	2·238
M. ruginodis .	9·248	1·613	10·659	1·859	11·139	1·943
1937						
L. flavus .	21·759	4·161	21·983	4·204	22·843	4·369
F. fusca. .	2·054	1·382	2·118	1·425	2·507	1·687
M. ruginodis .	9·541	1·997	9·804	2·052	9·718	2·034
1938						
L. flavus .	18·059	4·317	18·895	4·517	20·278	4·848
F. fusca. .	0·669	0·751	0·669	0·751	0·924	0·036
M. ruginodis .	18·065	5·042	18·925	5·254	19·043	5·315
1939						
L. flavus .	16·779	2·407	18·688	2·681	19·854	2·848
F. fusca. .	0·463	0·519	0·482	0·541	0·575	0·645
M. ruginodis .	13·579	2·841	13·633	2·854	13·751	2·878

7. WEIGHTS OF THE ANTS.

A full description of the technique used for weighing the living ants is given in Pickles (1937). After the censuses had been taken, the living ants were

TABLE 11.

Weights (in g.) of the ants from nests of *L. flavus*.

No. of nest	☿	♂	♀	Larvae	Naked pupae	☿ cocoons	♀ cocoons	☿ callows	Total
1936									
1	1·757	0·002	1·367	0·023	—	0·002	—	—	3·151
3	2·133	—	0·019	0·047	—	0·841	0·846	—	3·886
1937									
3	0·926	0·001	0·010	0·009	—	0·187	0·057	—	1·190
21	1·040	0·012	0·034	—	—	0·030	—	—	1·116
1	0·087	—	—	—	—	—	—	—	0·087
27	0·453	—	0·013	—	—	—	—	—	0·466
1938									
21	1·153	—	0·014	—	—	0·443	0·003	—	1·613
1	0·121	—	—	—	—	—	—	—	0·121
42	0·532	0·134	0·015	—	—	0·002	—	—	0·683
55	0·362	0·011	—	—	—	0·028	—	—	0·401
50	1·896	0·033	0·013	—	—	—	—	—	1·942
1939									
65	0·310	—	—	0·035	—	0·208	—	—	0·553
50	1·741	0·063	0·106	—	—	0·538	—	0·022	2·470
21	0·381	0·143	0·142	—	—	—	—	—	0·666

TABLE 12.

Weights (in g.) of the ants from nests of *L. fusca*.

No. of nest	☿	♂	♀	Larvae	Naked pupae	☿ cocoons	♀ cocoons	☿ callows	Total
1936									
6A	0·381	—	0·041	0·003	—	0·293	0·050	—	0·768
6B	0·395	—	—	—	—	0·985	0·050	—	1·430
17	2·405	—	1·158	—	—	0·377	—	0·071	4·011
13	0·508	—	0·041	0·124	—	0·644	—	0·015	1·332
19	0·050	—	—	—	—	—	—	—	0·050
15	0·157	—	—	—	—	—	—	—	0·157
2	0·691	—	0·042	0·111	0·579	0·400	—	0·045	1·868
1937									
30	0·851	—	0·024	0·094	0·321	0·311	—	—	1·601
31	0·997	—	0·010	—	—	0·017	—	—	1·024
36	2·163	—	0·095	—	—	0·163	—	—	2·421
37	0·342	—	—	—	—	—	—	—	0·342
1938									
34	0·979	—	—	—	0·247	0·361	—	—	1·587
1	0·121	—	—	—	—	—	—	—	0·121
43	0·362	—	0·027	—	0·066	0·063	—	—	0·518
44	0·035	—	0·029	—	—	0·006	—	—	0·070
46	1·076	—	—	—	—	—	—	—	1·076
1939									
70	0·245	—	0·028	0·023	0·077	0·016	—	—	0·389
71	0·253	—	0·025	—	0·005	0·057	—	—	0·340
46	0·138	—	0·027	—	—	0·031	—	—	0·196
34	0·557	—	0·028	—	—	0·027	—	0·001	0·613
64	0·056	—	0·028	—	—	0·012	—	—	0·096

TABLE 13.

Weights (in g.) of the ants from nests of *M. ruginodis*.

No. of nest	☿	♂	♀	Larvae	Naked pupae	☿ cocoons	♀ cocoons	☿ callows	Total
1936									
2	0·148	—	—	—	—	—	—	—	0·148
5	1·672	—	0·049	0·078	0·196	—	—	0·038	2·033
18	0·763	—	0·072	—	—	—	—	—	0·835
8A	0·518	—	—	0·057	—	—	—	—	0·575
21	0·074	—	—	—	—	—	—	—	0·074
1937									
29	0·195	—	—	0·290	0·110	—	—	—	0·595
8A	0·299	—	0·004	—	—	—	—	—	0·303
21	0·041	0·026	—	—	—	—	—	—	0·067
32	0·812	—	0·002	—	—	—	—	—	0·814
33	1·768	—	0·003	0·004	—	—	—	—	1·775
35	0·884	—	—	—	—	—	—	—	0·884
1938									
41	0·856	—	0·002	—	0·174	—	—	—	1·032
1	1·959	0·002	0·002	—	—	—	—	—	1·963
48	0·849	—	0·003	0·017	0·042	—	—	—	0·911
49	0·820	0·020	0·008	—	—	—	—	—	0·848
52	0·208	—	—	—	—	—	—	—	0·208
53	1·313	—	0·002	0·026	—	—	—	—	1·341
51	1·568	0·002	—	—	—	—	—	—	1·570
47	2·031	0·006	0·008	0·017	—	—	—	—	2·062

TABLE 13 (*continued*).

No. of nest	☿	♂	♀	Larvae	Naked pupae	☿ cocoons	♀ cocoons	☿ callows	Total
1939									
57	1·836	—	0·029	—	—	—	—	—	1·865
74	0·682	0·008	0·002	—	0·087	—	—	—	0·779
78	0·323	—	0·004	—	—	—	—	—	0·327
72	0·088	—	0·004	—	—	—	—	—	0·092
56	0·223	—	0·004	—	—	—	—	—	0·227
66	0·405	—	—	—	—	—	—	—	0·405

weighed. Analyses of the weights of the ants are given in Tables 11, 12 and 13. The variations in the total weights of the ants are given in Table 14 and fig. 4.

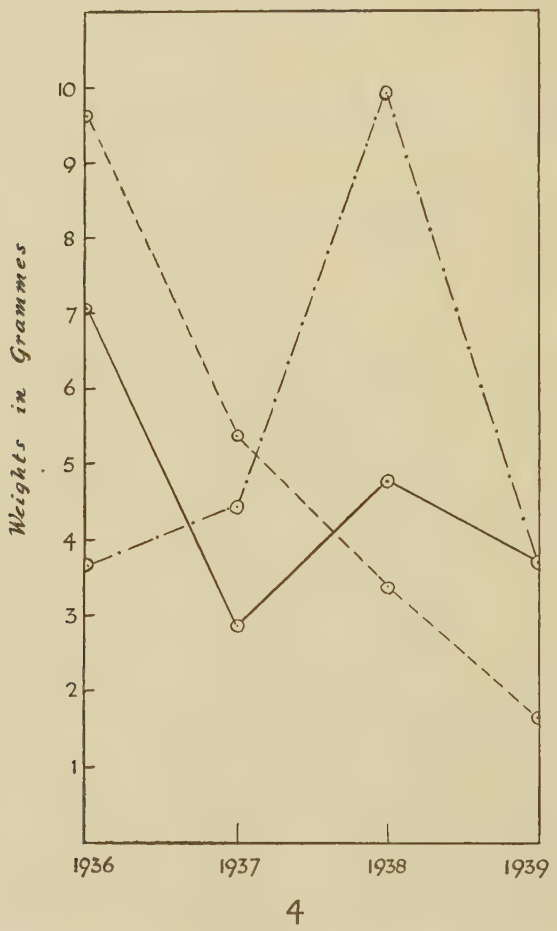

FIG. 4.—The fluctuations in the weights of the nest populations during the years 1936 to 1939. ——— *L. flavus*; — — — *F. fusca*; .—.—.— *M. ruginodis*.

Table 14.

The total weights (in g.) of the ant populations 1936–39.

Name of species	1936	1937	1938	1939
L. flavus	7·037	2·859	4·760	3·689
F. fusca	9·616	5·388	3·372	1·634
M. ruginodis	3·665	4·438	9·935	3·695

According to Gause (1934), the biological success or failure of a species living on a certain area can be judged by the weights of the living creatures besides the actual number of the population.

From Table 14 it is evident that the continued decrease in the population of *F. fusca* has manifested itself in a similar continuous decrease in weights. Of the three species, the weights of *L. flavus* have fluctuated most; whilst *M. ruginodis* has shown a peak of success in 1938. As regards weights, it seems that *L. flavus* and *M. ruginodis* were roughly equally successful in 1939, though they had a big difference of weight success in 1938 and in the first year when weighings were made.

8. The Biomasses of the Ants.

The success or failure of a species of ant may be expressed as the biomass, *i.e.* the total weight of biological material studied per unit area. As the weights of the ants were recorded in grammes, the square metre was used as the unit of area. The area of ground under investigation was 880·51 square metres in area.

Table 15.

The fluctuations in the biomasses of the ants in g. per square metre.

Name of species	1936	1937	1938	1939
L. flavus	0·008	0·003	0·005	0·004
F. fusca	0·011	0·006	0·004	0·002
M. ruginodis	0·004	0·005	0·011	0·004

The fluctuations of the biomasses of the ants show a considerable similarity to the weights as is to be expected.

From Table 15, the continuous decline in the success of *F. fusca* is manifest, as are also the great fluctuations of *L. flavus*, and the peak success of *M. ruginodis* in 1938 is also well shown.

9. Relations with other Insects, etc.

The insect in closest contact with the ants at Thornhill was *Tetraneura ulmifoliae* Bak. Theobald (1929) stated that it is found in the nests of all three species of ant met with in this survey. I have found it chiefly in association with *L. flavus* and *M. ruginodis*. It has possibly played a large part in the underground distribution of *L. flavus*. These ants have been found attending to the apterous viviparous females (Virgogenia) on the roots of the grass *Holcus mollis*. Evidently searching for the above aphis, many specimens of *Coccinella septempunctata* Linn. were found under the carpet of *Holcus mollis*.

Here also were found *Philonthus politus* Fab. and the woodlouse *Porcellio scaber*. Numerous specimens of *Campodea staphilinus* Westw. were often found beneath the stones of the ants' nests, particularly after rain. Donisthorpe (1927a) stated that there are no myrmecophilous species of Thysanura in Britain. I conclude that these insects are there purely accidentally, due to their habitat being under sods and stones. They were also plentiful under the *Holcus mollis* "carpet."

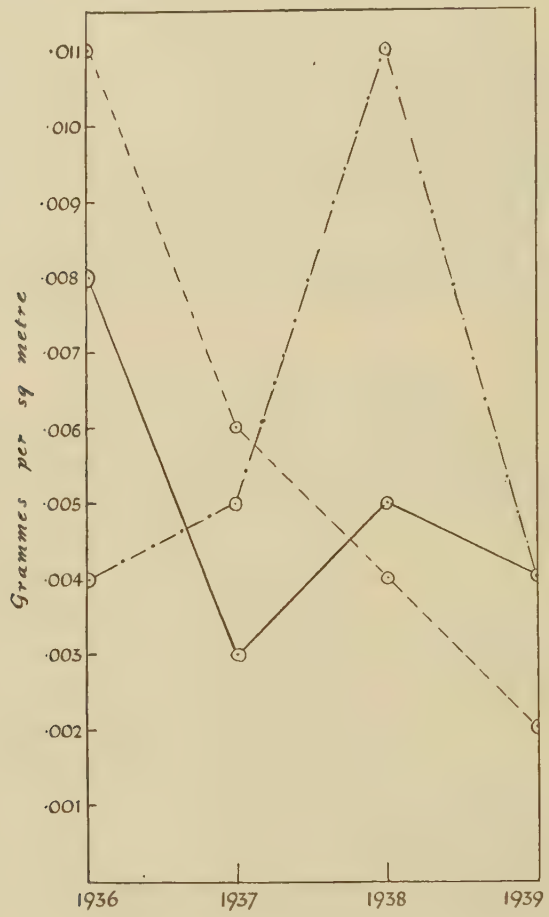

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Fig. 5.—The fluctuations in the biomasses during the years 1936 to 1939.
——— *L. flavus*; — — — *F. fusca*; ——·——·*M. ruginodis*.

Numerous specimens of the collembolan *Entomobrya multifasciata* Tbg., were found in the layer of decayed bracken fronds and amongst the lower parts of the tufts of grass.

On 13th April 1938 a mite *Gymnolaelaps* ? sp. n. was found on the gaster of a female *F. fusca*.

On several occasions, particularly in 1939, near some of the nests and stones, "droppings" of birds were found containing the remains of ants. These

" droppings " were identified as those of the green woodpecker (*Picus viridis pluvius* Hart.) by Mr. Ralph Chislett. This species of bird will therefore assist in keeping down the ant populations and act as a natural check on their activity.

10. Results of the Survey.

From this survey, several important points have come to light.

(a) *L. flavus :* Originally, there were two mounds of this species of ant. During the survey, these two nests disappeared; but the ruins have been re-inhabited by the same species of ant which must have migrated to the ruined mounds. These were nos. 1 and 3, and they were so persistent that they lasted during the greater part of the survey : no. 1 was re-inhabited even after it had disappeared in 1938. This seems to indicate that these nests are able to be recognised by these ants when once they have been inhabited by them.

It seems that the effect of repeated digging up of the nests of *L. flavus* is disastrous to the populations in that it causes them to decrease very much. Andrews (1929) stated that when he attempted to establish permanent nests of *Formica exsectoides* by transporting ants to another place, he was led to the conclusion that the mortality was great and that the conditions might be changed so much that they were caused to die off rather rapidly. This statement I found to agree with the results of repeated digging up of nests of *L. flavus* at Thornhill. The repeated digging up of the nests has tended to distribute the ants over the area under survey.

This method of studying the populations of the ants of this species hardly seems a suitable technique, as if the original nests had not been disturbed they would probably still have had a population of approximately 5000 each.

(b) *F. fusca :* Since 1936, when its populations were at their greatest, this species has gradually decreased in numbers. As with *L. flavus*, the continuous digging up of the nests possibly partly accounts for this decrease; but I believe that emigration and the small number of immature forms in the nests have also helped to cause this decrease.

(c) *M. ruginodis :* This species, having its greatest population in 1938, has also shown that considerable migration has occurred both on the area and to and from the surrounding region. This species and *L. flavus* are in competition to some extent on the area, as both species attend the aphis *Tetraneura ulmifoliae* on the roots of the grass *Holcus mollis.*

(d) Originally, both nests of *L. flavus* nos. 1 and 3 were covered with grass, chiefly *Aira flexuosa*; the surrounding region contains a mixture of this grass with *H. mollis.* Dr. Woodhead, who kindly identified the grasses for me, stated that *A. flexuosa* grows in drier spots than *H. mollis.* Donisthorpe (1927) mentioned that in many cases *L. flavus* builds its nest mounds so that they will be dry. It seems then that it is quite possible for the grass *H. mollis* to help in determining the positions of the nests of this species of ant (due to the aphis *T. ulmifoliae* being attended by them) and as a result of the dry nature of the soil of the nests, *A. flexuosa* grows on them. The latter grass is by no means confined to the mounds, as is stated earlier in the paper; but this may be due to the excellent natural drainage of the area, due to its steep slope.

Where mounds of *L. flavus* occur elsewhere on the hillside, they are all covered with *A. flexuosa*, which lends some support to the suggestions made above concerning the relationships of these grasses, ants and the root aphis *T. ulmifoliae.*

Diver (1938) said that *L. flavus* lives at its optimum in turf. The results at

Thornhill agree with this statement: the original nests of this species were covered with turf. He also mentioned (1938 : 132) that *F. fusca* shows a preference for bracken. There is thus a complete picture of the relationship of the environment to the distribution of the ants. The bracken has decided the presence of *F. fusca* on the area, and the grasses together with the root aphis (*T. ulmifoliae*) have determined the positions of the nests of *L. flavus* and to some degree those of *M. ruginodis*.

(e) One important fact emerges from this survey. That is, that actually the populations of each summer are practically separate from those of the preceding year. It may be granted that many of the ants of all three species will have continued to exist from one year to the next, but the majority of the ants appear to have been migrants possibly from the surrounding area. It seems quite definite that the whole population of the area is in a constant state of flux, ants migrating about on the area itself and to and from the surrounding area.

11. Acknowledgements.

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12. Summary.

1. A survey of three species of ant living on a hillside at Thornhill, Yorkshire, was carried out during the summer months of the years 1935 to 1939.

2. Territories of the ants. By following the ants from their nests and measuring the maximum distances travelled by them, their foraging territories were calculated, namely 236 sq. yds. for *Formica fusca* and 36·7 sq. yds. for *Myrmica ruginodis*: by digging up the soil round nests of *Lasius flavus* and obtaining maximum distances travelled underground by these ants, the foraging territory of 50·3 sq. yds. was calculated.

3. Populations. By digging up the nests and counting the living inhabitants, the fluctuations in populations during the five years of the survey were recorded. The peak populations for each species were in 1935 for *L. flavus* (with a second peak in 1938); in 1936 for *F. fusca* and since then there has been a continuous decrease in population. For *M. ruginodis* the greatest population was in 1938.

4. Densities of population. These are set out in detail in Table 7. The highest Economic Density for *L. flavus* occurred in 1935, for *F. fusca* in 1937 and that for *M. ruginodis* in 1935 and 1938. The greatest Lowest Densities were recorded for *L. flavus* in 1935, for *F. fusca* in 1936 and 1937 and that for *M. ruginodis* in 1938.

5. Weights and biomasses. Weighings of the living ants were commenced

in 1936. After each permanent nest had been counted, the living inhabitants were weighed. The biomasses were then calculated from these weights. The weights show a maximum for *L. flavus* in 1936, for *F. fusca* in 1936, and for *M. ruginodis* in 1938. The biomasses give the maximum weights per unit area for the respective species for the same years. This means that during these particular years, when the maxima occurred, this or that particular species was the most successful on the area at that time.

6. General. From a study of the population tables and from actual observations made on the area, it seems that the ants are continually moving about on the area and migrations to and from the surrounding land must occur. The population of *L. flavus* nests seem to suffer most by the repeated digging up, though they appear to retain possession of old nests longer than the other two species. This may be due to the recognition of an old nest mound by the chemical nature of the saliva in altering the pH of the nest soil by making it more alkaline than the soil surrounding the mound.

References.

Andrews, A. E., 1929, " Populations of ant mounds." *Quart. Rev. Biol.* **4** : 248–257.

Bodenheimer, F. S., 1938, *Problems of animal ecology.* Oxford.

Carey, E., and Diver, C., 1937, " Territory in the yellow field ant (*Acanthomyops flavus*)." *J. anim. Ecol.* **6** : 193–194.

Diver, C., 1938, " The plant-carpet in relation to animal distribution." *Proc. Linn. Soc. Lond.* **1938** : 124–135.

Donisthorpe, H. St. J. K., 1927, *British ants.* London.

——, 1927a, *The guests of British ants.* London.

Elton, C., 1932, " Territory among wood ants (*Formica rufa*) at Picket Hill." *J. anim. Ecol.* **1** : 69.

Gause, G. F., 1934, *The struggle for existence.* Baltimore.

Imms, A. D., 1934, *A general textbook of entomology,* 3rd ed. London : 149.

Janet, C., 1898, " Reaction alcaline des chambres et galeries des nids de fourmis." *C.R. Acad. Sci. Fr.* **127** : 130–133.

Lubbock, J., 1888, *Ants, bees and wasps,* 9th ed. London : 9.

Pickles, W., 1936, Populations and territories of the *Formica fusca*, *Acanthomyops flavus* and *Myrmica ruginodis* at Thornhill (Yorks)." *J. anim. Ecol.* **5** : 262–270.

——, 1937, " Populations, territories and biomasses of ants at Thornhill, Yorkshire, in 1936." *J. anim. Ecol.* **6** : 54–61.

——, 1938, " Populations, territories and biomasses of ants at Thornhill, Yorkshire, in 1937." *J. anim. Ecol.* **7** : 170–180.

——, 1940, " The effects of ants on the acidity of the soil." *Ent. mon. Mag.* **76** : 49–52.

Theobald, F. V., 1929, *The plant-lice or Aphididae of Great Britain* **3** : 299.

Wigglesworth, V. B., 1927, " Digestion in the cockroach, (1) The hydrogen ion concentration in the alimentary canal." *Biochem. J.* **21** : 791–796.